PROCEEDINGS
OF THE
NATIONAL ACADEMY OF SCIENCES

Volume 16 May 15, 1930 Number 5

ON THE DISTRIBUTION OF TABULAR ROOTS IN CEIBA (BOMBACACEAE)[1]

By A. E. Navez

Laboratory of General Physiology, Harvard University

Communicated March 26, 1930

I. The presence of tabular roots, often called "buttresses," has long been noted by naturalists, especially in connection with tropical trees. Descriptions and pictures show roots of this type to occur frequently in very different families, and that they are not specific characters for the plants considered. Their occurrence is especially noticeable in regions where the superficial layers of soil are relatively thick and present little resistance for anchorage; they are found also in places where the top layers of humus soil are very thin and are supported directly by a rocky basement. These two types of stations are very well represented by the conditions found in the "varzea" grounds of the Lower Amazon district and by the "Seboruco" patches of Cuba.

In the Lower Amazon district the presence of large quantities of water in an alluvial region determines a soil which offers little resistance to the extraction of roots when trees are subjected to high winds, unless the trees have very deep-reaching roots.

The second case offers another example where the conditions of anchorage are quite as poor as in the first, but here due to lack of the possibility of any deep grip.

The characters of these two habitats show in fact two extreme cases of anchorage of big vegetal masses offering large surfaces for the action of the wind. The engineering problem of anchorage has received several solutions by plants (*cf.* Navez, 1924).[2] Among these solutions two are of special interest; they can be characterized as follows:

(1) Tabular roots of the rectangular triangle type, the longest side of the right-angle being vertical and the hypothenuse side being very steep. They do not spread very far from the trunk of the tree. (2) Tabular roots originating at low height (20–60 cm.) and spreading over great distances, more or less radially from the trunk. The first type is found,

for instance, in *Glycoxylon grande* (Ducke) and in *Dipteryx odorata* (Willd) in the Lower Amazon region, also in *Ceiba pentandra* (Gaertn) in Amazonia and Cuba. The second type is well represented by *Ficus* (div. sp.) in Amazonia and Cuba, as well as by *Erythrina glauca* (Willd) and *Parkia pendula* (Benth) in Amazonia. Intermediates can be found, but they may be only young stages of the triangular type.

Generally in regions where trees with tabular roots are found the two types occur. One could point out that the first type seems dominant in regions presenting the "varzea" character and that, on the contrary, the second type occurs more frequently in soils with little depth. Nevertheless this rule is far from being absolute, especially if one takes into account the fact that each type of tabular root seems to be proper to a certain number of species. In a rather extensive series of observations made in Brazil and in Cuba we have not found that the same species could produce indifferently the one or the other type. In fact, it is not the root formation which is a specific character, it is rather the *type* of tabular root which seems characteristic for groups of genera or of species as well.

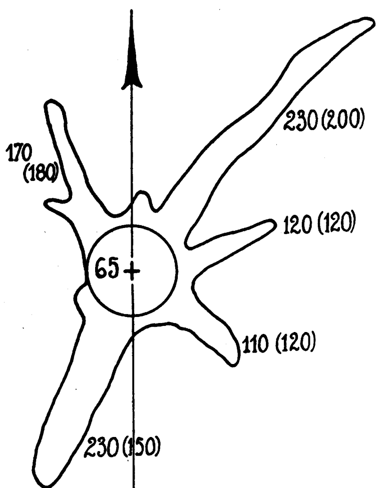

FIGURE 1

Distribution-pattern of tabular roots of *Ceiba pentandra* (Gaertn), a tree on the road to Guabairo (near Cienfuegos, Cuba). The figure inside the circle gives the diameter of the tree at 1.50 m. above the ground level. The figures 230 (200) along the roots indicate respectively the horizontal and vertical distances at which the roots extend from the trunk (above the surface of the ground).

II. The distribution of tabular roots seems at first sight to be at random; it is so to the person who passes from one region to another. The massing of data collected during a trip is therefore not legitimate, especially if they were collected in very different localities on different grounds and with varying conditions of exposure.

One may think, nevertheless, that the distribution is necessarily induced by some mechanical factor acting in moving the mass of the whole tree. This fact is indicated clearly by the presence of one or several dominant roots on the one side of the tree which is above it, if we consider a tree placed on the slope of a hill. The gravitational factor effective as a tendency to pull the tree down is counteracted in this case by the presence of resistance-elements playing the role of the cables anchoring a tall structure to the ground. In flat regions, where this gravitational factor is acting equally in all directions if the tree is perfectly vertical, another agent must come into play. The wind has been pointed to as this agent. The previously available data (Navez, 1924; Ghesquiere, 1925[3]) are of a purely qualitative character, and furthermore we have not been able to correlate definitely the distribution of the roots with the directions of the winds. In the work of G. Senn (1923)[4] on *Populus nigra italica* the author

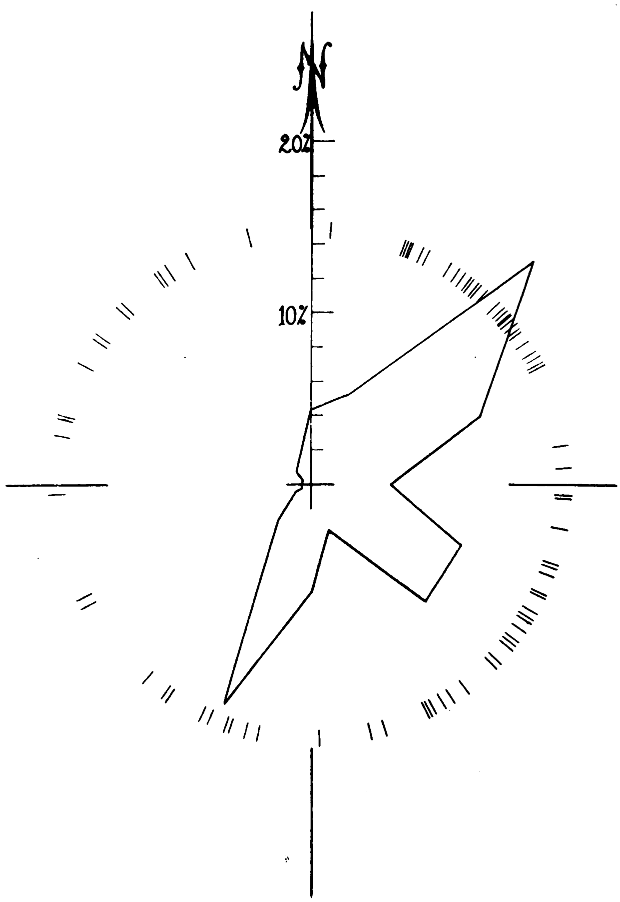

FIGURE 2*a*

Polygon of wind-frequency as percentage of total occurrence. The short lines disposed in a circle indicate the observed positions of tabular roots.

correlated the presence of rather small tabular roots in a roughly quantitative way with dominant winds. It was thought, therefore, interesting to select a certain number of trees placed as much as possible under identical conditions in a small area, for which meteorological data were existent, and to test this correlation. We chose samples of *Ceiba pentandra* (Gaertn) (Bombacaceae) in the vicinity of Cienfuegos (Province of Santa Clara), Cuba. The specimens were as similarly located as possible, i.e., on an horizontal surface, and as much as possible well isolated from other big trees. It was found that the presence of small trees and underbrush (as in the rocky outcrops called seborucos) did not introduce any special effect on the distribution of roots.

This type of tree is particularly well suited for such observations on account of the propensity it shows to produce tabular roots (3, 4, 5 and even 6 *per* tree), and also by the fact that *Ceiba*, being a tree much venerated by the inhabitants, is always left standing even if the rest of the forest has been burned down or cut away. The selection of this region for the collection of data was determined principally by the existence of a fairly extensive series of meteorological data, made with the utmost care, and published from 1911 on in the Anales del Observatorio del Colegio Ntra Sra. de Montserrat in Cienfuegos.[5]

For all the observed trees, 28 in number, a distribution pattern of the roots was made (for a typical one, see figure 1), taking care to record care-

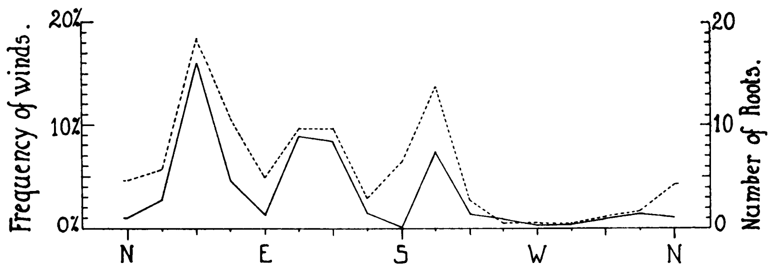

FIGURE 2*b*

The wind-frequency plot (interrupted line) and the distribution of tabular roots (solid line) showing correlation existing between the two.

fully the cross-section of the tree, the radial extension of the roots, and the vertical heights reached along the trunk. All other indications, as presence of rock outcrops, etc., were also recorded.

For the area studied (about 30 sq. miles) the axes of the tabular roots were determined from the pattern and transferred to a mass-plot.

On the other hand, the annual metereological tables were reduced to means and a polar frequency distribution plot of these values as percentage of the total occurrence of wind directions was made (Fig. 2a).[6]

When the two plots are superimposed one upon the other, as in figures 2a and 2b, a very good agreement is found between the two distributions. The frequency of occurrence of tabular roots corresponds entirely with the frequency distribution of the dominant winds. If we remember that in the plots the wind is supposed to come from the quarter considered and fly in the direction of the center of the "wind rose," we must also note that the tabular roots of the trees are located precisely on the sides of the tree-trunks which are directly exposed to the wind action. This is then in absolute contradiction with the property formerly ascribed to these tabular roots by giving them the name of buttresses. They act as *resistance cables* indeed, and not as buttresses against a wall.

In all the trees the roots were unequal: one root (rarely two) is definitely larger than the others. If our interpretation is correct, we ought then to find the position of this particular root to be correlated with the direction of the dominant wind; in fact, in 94% of the cases, the root with the largest mass and largest insertion-radius was found on the side corresponding to the direction of the strongest wind.

This second fact reinforces the idea of considering the roots as traction-resistant and not as compression-resistant structures. The presence of additional tabular roots does not at all diminish the importance of the main ones. In fact, even when the wind is blowing from the dominant quarter, its action is not localized in a sharp and unique direction, and a certain distribution of pulls must surely result.

In the region here considered, these dominant winds are the trade winds blowing in a rather steady way from NE and ENE. It is to be remarked also that in the same region from about 11 A.M. the ordinary wind swings around from E-ESE to S and SW, where it remains up to late in the day, unless some atmospheric perturbation brings it over to another quadrant. At the start of the night the land breeze rises from NE, which blows with decreasing strength up to the rise of the sun. The regularity of these winds is in fact a very remarkable feature of this region. This may account then for the close correlation existing between the distribution of tabular roots and of dominant winds.

Summary.—From comparison between detailed meteorological data regarding dominant winds and the distribution pattern of tabular roots of *Ceiba pentandra* in Cuba the following conclusions are drawn:

(1) The tabular roots are located principally on the sides of the dominant winds; the largest is generally located in the NE-ENE direction.

(2) These roots act as resistance-cables and not as "buttresses."

(3) The dominant winds are the factor determining the growth of these tabular roots.

[1] The observations on *Ceiba* were made while at the Harvard Biological Station at Soledad, Cienfuegos, Cuba (September, 1928).

[2] Navez, A. E.. *Bull. Soc. R. Bot. Belg.*, **57**, fasc. 1, 7–17 (1924).

[3] Ghesquiere, L., *Rev. Zoöl. Afric.*, **13,** 2 Suppl. Bot. B. 1 (1925).

[4] Senn, G., *Verh. Naturf. Ges. Basel.*, **35,** 1, 405 (Festband H. Christ) (1923).

[5] For sending data and useful information in connection with it, the author is very much indebted to R. F. Santiago M. Viña S. J. of the Colegio de Montserrat.

[6] We had thought that it would be possible to use the wind distribution diagrams of the Monthly Pilot-Charts for the Central American waters. as published by the Hydro-

graphic Office of the Navy Department, especially because four of these diagrams (placed in a square of $2^1/_2$ degrees) cover fairly well the whole region of which Cienfuegos is the center. Unfortunately, the data collected and treated as already indicated do not seem to agree adequately with the events registered at the Observatory of Montserrat. They show nevertheless the same general dominant direction of the wind but do lack one of the secondary maxima. As all our data have been collected in the near vicinity of Cienfuegos, we have preferred to base our deductions on the more detailed records made by the Observatory.

ACTION CURRENTS IN THE AUDITORY NERVE IN RESPONSE TO ACOUSTICAL STIMULATION

BY ERNEST GLEN WEVER AND CHARLES W. BRAY

PSYCHOLOGICAL LABORATORY, PRINCETON UNIVERSITY

Read before the Academy April 28, 1930

This experiment was planned in the effort to discover an answer to certain fundamental questions of auditory theory through a determination of the relationship obtaining between the character of the response of the auditory nerve and the frequency and intensity of sound affecting the ear. The cat was selected as the experimental animal, and the investigation consisted of placing electrodes on the exposed auditory nerve, and detecting the action currents in the nerve resulting from stimulation of the ear by sound.

Procedure.—The procedure was as follows: After decerebration under deep ether anesthesia by the trephine method, the skull was opened sufficiently to gain access to the right auditory nerve. An electrode, which usually took the form of a small wire hook, was then placed around the nerve, while a second electrode was placed elsewhere on the body, usually on the severed tissue of the cerebrum.

The currents picked up by these electrodes were conducted through 60 feet of shielded cable to a vacuum tube amplifier located in a soundproof room and, after amplification, were led to a telephone receiver. The ear of the animal was then stimulated, and the resulting nerve impulses detected as sound by an observer listening at the receiver in the soundproof room.

Results.—The results so far obtained in this investigation bear upon the question of the relation between the qualitative aspect of the stimulus and the nature of the nerve response. It was found that sound stimuli applied to the ear of the animal set up in the auditory nerve action currents of frequencies corresponding to those of the sound waves. These action currents, after amplification, were audible in the receiver as sounds